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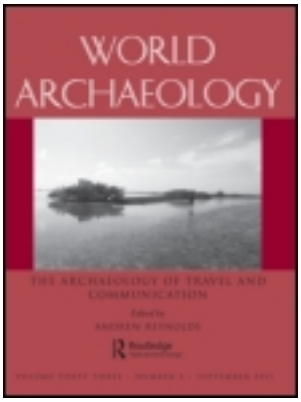

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The impact of the dingo on the thylacine in Holocene Australia

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The impact of the dingo on the thylacine in Holocene Australia

Melanie Fillios, Mathew S. Crowther and Mike Letnic

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Abstract

The thylacine (*Thylacinus cynocephalus*) was one of Australia's largest predators, but became extinct in mainland Australia soon after the arrival of a new predator, the dingo (*Canis lupus dingo*) around 3500 BP. Evidence implicating the dingo in the thylacine's extinction has been equivocal, largely because thylacines are thought to be considerably larger than dingoes. Thus, other concurrent factors, such as shifts in human technology and population increase as well as climate change, have been cited to explain their extinction. Here we present new morphological evidence that female mainland Holocene thylacines were actually smaller than dingoes. We discuss these findings against archaeological and contemporary ecological evidence concerning dingoes' environmental impacts, and provide evidence that, as novel predators, dingoes induced a trophic cascade that had dramatic impacts on the fauna and economy of Holocene Australia. We suggest that dingoes, owing to their larger brains and body size, were likely a primary agent for the extinction of the thylacine from mainland Australia.

Keywords

Extinctions; Australia; thylacine; dingo; ecology; archaeology.

Introduction

Faunal extinctions have received considerable attention in Australia, but with a notable exception (Johnson 2006), few of these studies have taken an interdisciplinary approach to the examination of their causes. Pleistocene extinctions have garnered much of the attention, with popular debate tending to polarize the causes, often in quite an acrimonious fashion – generally favouring either an anthropogenic (e.g. Flannery 1994; Johnson 2006; Miller et al. 2005; Roberts et al. 2001) or a natural driving force (Price et al. 2011) explanation, with few authors favouring a more multi-causal hypothesis (Field et al. 2008; Flood 1999; White and O'Connnell 1982; Wroe et al. 2004). Holocene species extinctions, while certainly less numerous, have been the subject of less heated debate, with

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the thylacine (*Thylacinus cynocephalus*) and Tasmanian devil (*Sarcophilus harrisii*) (Archer 1974; Johnson and Wroe 2003; Jones and Stoddart 1998; Paddle 2000; Wroe et al. 2007) receiving much of the focus.

This study uses a multi-disciplinary approach, integrating archaeological, palaeontological and ecological data to revisit the extinction of the thylacine, or Tasmanian tiger (*Thylacinus cynocephalus*). The thylacine is thought to have become extinct on the Australian mainland *c*. 3500 BP, with late survival on the island of Tasmania until the early twentieth century. Various explanations have been forwarded as a cause of its extinction, the two most popular being people in the form of intensification (see below) and the introduction of the dingo (*Canis lupus dingo*) (cf. Archer 1974; Corbett 1995; Wroe et al. 2007). However, both explanations have suffered from sparse physical supporting evidence, and so the cause(s) of the extinction of the thylacine has remained speculative.

In this paper, we present new data supporting the view that the introduction of a new predator *c*. 3500 BP could indeed have caused the thylacine's extinction on the mainland. Using new morphological data gathered from Holocene thylacines from mainland Western Australia, one of the few areas in which there appears to be a well-dated chronological overlap between the two species (Johnson 2006: 154–5), we show that during the Holocene mainland female thylacines were significantly smaller than either their larger bodied Tasmanian or their mainland Pleistocene counterparts. We suggest that this Holocene dwarfing, coupled with the introduction of a novel predator, the dingo, likely facilitated the ultimate extinction of the thylacine on mainland Australia. We then pair these findings with archaeological evidence from several Australian Holocene faunal assemblages to further examine the influence this new predator might have had on prey species, suggesting that dingoes could also have played a key role in the shift toward smaller body-sized prey being exploited by people.

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Background

History of the thylacine

Until the late Holocene, the thylacine, a marsupial, was one of Australia's largest terrestrial predators, becoming extinct on mainland Australia soon after the arrival of a morphologically convergent placental predator, the dingo *c*. 3500 BP (Corbett 1995; Gale 2009; Johnson and Wroe 2003). Since the disappearance of the thylacine and another marsupial predator, the Tasmanian devil, was coincident with the arrival of the dingo, most surmise that dingoes caused their extinctions through competition, either for food resources and/or through direct confrontation (Corbett 1995; McNab 2005; Wroe et al. 2007). Some, however, have rejected this view (Johnson and Wroe 2003; Paddle 2000), generally based on the fact that Tasmanian thylacines were considerably larger than dingoes (some estimates put male Tasmanian thylacines at twice the mass of dingoes). Additionally, morphological differences between thylacines and dingoes suggest they would have likely occupied very different niches, with the thylacine a more specialized carnivore (Johnson and Wroe 2003). People and disease have also been variously cited as possible factors (Johnson 2006; Johnson and Wroe 2003; Paddle 2000).

History of the dingo

The dingo is a primitive domestic dog descended from the Asian wolf (Corbett 1995). Mitochondrial DNA evidence suggests that the dingo arrived in Australia approximately 5000 BP (Savolainen et al. 2004), and would likely have spread throughout the continent within 100 years of its arrival (Saunders et al. 1995). The oldest fossil evidence of dingoes in Australia is dated to 3500 BP (Corbett 1995).

The geographic origin of the dingo is still debated, as is the time of its introduction. The earliest skeletal evidence for dingoes in Australia ranges from 3500 to 3000 BP, and has been uncovered in a variety of geographic locations: from sites in Western Australia (Madura Cave, Nullarbor 3450 BP) (Milham and Thompson 1976), New South Wales (Wombah Midden, 3230 BP) (McBryde 1982),and Victoria (Fromm's Landing, 3170 BP) (Mulvaney et al. 1964). Dingoes likely originated in Southeast Asia (Indonesia, Papua New Guinea), as they have close genetic affinity to the New Guinea Singing Dog (Savolainen et al. 2004), and were likely brought to Australia by people, either as a product of trade or via commensal relationships. The absence of dingoes from the island of Tasmania, isolated from mainland Australia after 12,000 BP by rising sea levels, lends further weight to their introduction by people.

Holocene Australia

Intensification Holocene Australia (*c*. 10,000 BP to the present) is characterized by several significant changes, particularly during the last 5000 years (see Johnson and Brook 2011). These changes are frequently encompassed by the term 'intensification' (Lourandos 1983), and include demographic changes suggestive of an increase in population such as a higher frequency of archaeological sites and artefact densities (e.g. Attenbrow 1987; Hughes and Lambert 1982; Johnson and Brook 2011; Lourandos 1983; McConnell and O'Connor 1999; Morwood 1987; Ross 1985; Smith and Ross 2008), a change in human technology, characterized by what is often termed 'the Small Tool Tradition' (backed blades, points, tulas, adzes) (Gould 1969) and a shift in prey species to smaller body sizes (Dortch 2004a, 2004b; Dortch and Wright 2010; Morwood 1987). The driving forces behind these cultural and technical changes are still debated, with changing subsistence strategies aimed at risk reduction (Hiscock 1994) and climate change both sited as factors (Dortch 2004a, 2004b; Dortch and Wright 2010; Johnson and Wroe 2003). Despite the debate over causality, Australian archaeologists agree that several significant changes occurred in Aboriginal culture during the late Holocene, and these changes are intricately tied to a changing relationship between people and their environment.

Climate While fine-resolution palaeo-environmental data for Holocene Australia is thin, data from deep sea and lakebed cores show a basic trend of increasing aridity over the past 15,000 years (Gingele et al. 2007). There appears to be an arid interval between 8000 and 5000 BP (Kershaw 1995), with the last 5000 years experiencing a relatively stable climate, interspersed with periods of high rainfall. A small fluvial pulse occurs around 3000 BP, but rapid large-scale fluctuations in lake salinity at Lake Keilambete indicate varying climatic

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conditions with short dry and humid events (Gingele et al. 2007). This pattern differs little from the present-day affects of ENSO (Moy et al. 2002). It may be argued, therefore, that that climate change is not likely to have played a role in extinctions during the last 5000 years.

Species extinctions The terrestrial mammal fauna of Australia was transformed during the Holocene during two waves of extinctions. The first wave of extinction occurred approximately 3500–1500 BP, around the time that the dingo arrived and saw the extinction of the mainland's largest land predators, the Tasmanian devil and the thylacine (Johnson 2006). These extinctions also coincided with the disappearance of a large flightless bird, the Tasmanian native hen (*Gallinula mortierii*) (Baird 1991).

The next wave of extinctions began in 1788 with the arrival of British colonists in Australia. The colonists introduced many species of animals for a range of purposes, including production/subsistence, domestic companions, hunting and for the aesthetic purpose of simply seeing and hearing them (Rolls 1969). The settlers also brought accidental invaders such as rats and mice as stowaways on arriving ships. Two of these introduced species have had devastating impacts on the continent's fauna: the red fox (*Vulpes vulpes*) and the feral cat (*Felis catus*). These predators have been implicated in the extinction of native rodents and marsupials weighing between 0.05 and 10kg, throughout the continent, but particularly in the arid zone (Letnic et al. 2009).

Until now, the assumption has been that all thylacines were similar to the large-bodied specimens known from Tasmania, even though previous studies indicated great geographical variation in thylacine size (Dawson 1982; Lowry 1972). Thus, despite the many studies examining the extinction of the thylacine, none has actually measured extant Holocene thylacine material from mainland Australia.

Methods

Endocranial volume was used to provide an estimate of body size in both thylacines and dingoes. Canine tooth strength was used as an indicator of prey size. Measurements were taken on crania and teeth from twelve dingo and twelve thylacine specimens, from Holocene deposits from south-west Australia and the Nullarbor region of Western Australia, held in the palaeontology collection in the Western Australian Museum (WAM) in Perth (Table 1). Measurements were limited to adult specimens, aged by permanent dentition, specifically eruption of the permanent third molar, and synostosis of the occipito-sphenoidal suture on the skull, after Macintosh (1975). In order to estimate brain size, endocranial volume was measured by inserting 6mm acrylic beads through the foramen magnum, following Wroe et al. (2003). These relatively large beads were used to ensure that beads were not trapped inside the skulls of the fossil specimens. A Student's *t*-test was used to compare differences between endocranial volumes of Holocene dingoes and thylacines.

In order to calculate canine strength, measurements taken were the crown height of the canine tooth, medio-lateral diameter of the canine tooth and the anterior-posterior diameter of the canine tooth (Jones 1997; Van Valkenburgh and Ruff 1987). In order to

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Table 1 Holocene specimens examined held in the palaeontology collection, the Western Australia Museum (WAM), Perth, Western Australia.

WAM accession number	*Species*	*Site*	*Location*	*ECV*	*Canine strength S_x*
76.9.385	Dingo	Liberation cave	Southwest	90	6.6372
76.9.384	Dingo	Liberation cave	Southwest	85	2.7117
65.12.104	Dingo	Witchcliffe Rockshelter	Southwest	81	1.9641
f6342	Dingo	Thylacine hole	Nullarbor	65	1.8380
63.3.25	Dingo	Lake Cave	Southwest	75	2.3979
b3227a	Dingo	Lynch Cave 3	Nullarbor	–	2.4990
64.2.4a	Dingo	Augusta-Marg	Southwest	–	2.4478
60.8.2	Dingo	Dingo Cave	Southwest	–	2.3654
62.3.1	Dingo	Boranup	Southwest	–	2.5693
67.9.138	Dingo	Cave near MA	Nullarbor	–	1.8697
68.4.1	Dingo	Eucla Basin	Nullarbor	–	2.7793
62.2.4b	Dingo	?	Nullarbor	–	3.0334
f63.55	Thylacine	Thylacine hole	Nullarbor	43	–
f6358	Thylacine	Thylacine hole	Nullarbor	30	1.3455
f6354	Thylacine	Thylacine hole	Nullarbor	40	2.4413
f6353	Thylacine	Thylacine hole	Nullarbor	40	–
69.12.4	Thylacine	Skull Cave	Southwest	40	–
64.8.1	Thylacine	Murra-el-elevyn Cave	Nullarbor	–	1.5584
61.2.34	Thylacine	Augusta	Southwest	–	3.0033
76.10.481	Thylacine	Skull Cave	Southwest	–	1.9286
65.12.18	Thylacine	?	Southwest	–	1.8531
65.8.5	Thylacine	Augusta east	Southwest	–	4.5095
76.3.1	Thylacine	Yallingup	Southwest	–	1.9049
99.10.4	Thylacine	?	Nullarbor	–	1.5346

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compare the placental dingo to the marsupial thylacine, and as dasyurid teeth grow throughout life (Jones 1997), canine height was measured from the junction of the tooth with the skull following Jones (1997) rather than the dentine-enamel junction used by Van Valkenburgh and Ruff (1987).

Canine strength (S_x) was calculated following Van Valkenburgh and Ruff (1987) and Jones (1997) using the equation:

$$S_x = Ix/Fhb,$$

where h = crown height of the canine tooth, F = force (set at one) and b = half the maximum medio-lateral diameter of the canine tooth, and:

$$Ix = (\pi ab^3)/4,$$

where a = half the maximum anterior-posterior diameter.

A two-way ANOVA was used to compare differences between dingoes and thylacines at both south-west and Nullarbor locations.

Species frequencies from ten Holocene archaeological deposits were also examined to test whether dingoes might have also affected other prey populations, thus explaining the shifts towards smaller prey observed in the archaeological record (see above). To mitigate the possible effects of cultural/biogeographical diversity, sites were intentionally chosen from a variety of locations around Australia (Table 2). Species were grouped by body size (large >5 kg), and then according to date. Using 3500 BP as the date for the arrival of dingoes, the analysis was restricted to sites that had strata that were dated pre- and post-dingo, contained more than ten MNI (minimum number of elements) and had associated stone artefacts. Frequencies were averaged from each temporal group/site to account for differences in reported quantification methods (e.g. NISP vs. MNI). The three temporal categories were then compared to one another, and to other sites. As the archaeological data for these assemblages showed a trend towards smaller body sizes in the strata in which dingoes were known to be extant (Fig. 1a), statistical modelling was performed using a generalized estimated equation (GEE) model (Hardin and Hilbe 2003) with an hypothesis-testing approach. A comparison of the frequency of large prey over time against several 'effects' was carried out: rainfall, presence/absence of dingoes, latitude, strata, abundance of stone artefacts, rainfall and dingoes. There was a strong interaction between dingoes and rain, and this interaction was modelled to generate a predicted frequency of prey body size (Fig.1 b).

Results

Morphological evidence suggests that female mainland thylacines were on average smaller than dingoes. Endo-cranial volume was significantly greater in dingoes than thylacines (Fig. 2; $t = 10.91$, $df = 19$, $p < 0.001$). While the mean torsional strength of the canine was

Table 2 Archaeological sites examined containing dated Holocene faunal deposits (pre- and post-3500 BP).

Site	*Location*	*Reference*
Devon Downs Rockshelter	South Australia 34° 38' S, 139° 38' E)	Smith 1982
Serpent's Glen	Carnarvon Range, Western Desert (25°13' S, 120°44' E)	O'Connor et al. 1998
Juukan 2	Pilbara, Western Australia (22° 26' S, 117° 19' E)	Slack et al. 2009; Fillios unpublished
Cathedral Cave	Queensland (23° 20' S, 148° 07' E)	Beaton 1991
Walkunder Arch Cave	Cape York Peninsula, North Queensland (144° 31'E, 17° 13's)	David 1984
Platypus Rockshelter	SE Queensland (27° 21' S, 152° 36' E)	Hall and Hiscock 1988
Skull Cave	Western Australia (34° 17' S, 115° 06' E)	Porter 1979
Nawamoyn	Arnhem Land, NT (12° 23' S, 132° 56' E)	Schrire 1982
Malangangerr	Arnhem Land, NT (12° 27E, 132° 57S)	Schrire 1982
Tunnel Cave	Western Australia (34° 13' S, 115° 02' E)	Dortch and Wright 2010

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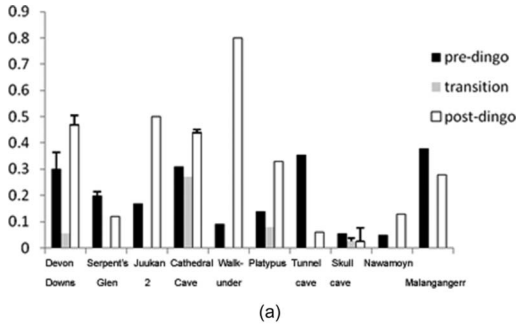

Figure 1 (a) Change in frequency of prey body size over ten archaeological Holocene cave deposits during three periods: pre-dingo (>3500 BP), transition (undated) and post-dingo (<3500 BP). (b) Predicted change in frequency of prey body size with interaction of dingoes and rainfall (fitted GEE).

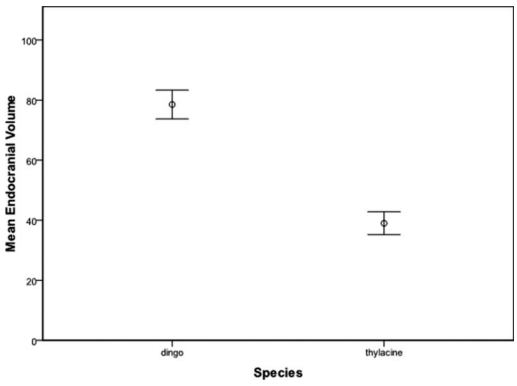

Figure 2 Comparison of mean endocranial volume between dingoes and thylacines. Error bars depict standard errors (95 per cent CI). $t = 10.91$, df = 19, $p < 0.001$.

slightly higher for dingoes than thylacines, the difference was not found to be statistically significant (Fig. 3; $_{F1,17} = 1.05$, $p = 0.320$).

The results of the hypothesis-testing approach examining the change in mammal body-size frequency suggest that the interaction between dingoes and rainfall had the greatest effect on the frequency of prey body size. Single factors, such as the frequency of stone artefacts, precipitation and dingoes were not found to be predictors of the frequency of prey body size. The model suggests that the combination of the presence/absence of dingoes and rainfall levels exerted the strongest influence on shifts in body size observed in Holocene faunal assemblages (Fig. 1b) (e.g. dingoes will have the greatest effect – or at least the most visible effect in areas of higher precipitation).

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Discussion

Morphological data suggest that there were significant differences in the size of Tasmanian thylacines compared with their mainland Holocene counterparts, with brain size reduced to nearly half that of their larger relatives (Fig. 4). While there are no complete Holocene skulls or suitable skeletal material from other locations in Australia, teeth collected in south-east Australia (Macintosh and Mahoney 1964), and examination of a damaged cranial specimen from north-west Australia (Cape Range: Kendrick and Porter 1973), indicate that the trend for mainland thylacines to be smaller than their Tasmanian conspecifics during the Holocene was not restricted to south-west Australia (Dawson 1982). This difference in size may therefore provide the missing evidence to support a role for dingoes in the extinction of the thylacine, also calling into question the applicability of using inferences based on Tasmanian and Pleistocene data in mainland Holocene contexts.

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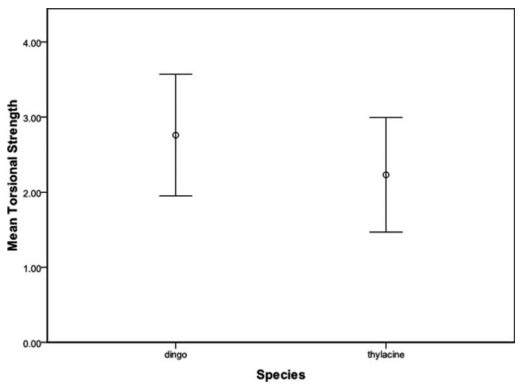

Figure 3 Comparison of mean estimates of the torsional strength of canines between dingoes and thylacines. Error bars depict standard errors (95 per cent CI). $t = 1.03$, $df = 19$, $p = 0.32$.

Figure 4 A comparison of the skulls of thylacines (left WAM F6358 and centre WAM F6353) and a dingo (far right WAM 68.4.1) depicting size differences between mainland Holocene species from sub-fossil deposits from the Nullarbor region of Western Australia. The thylacine on the far left is thought to be a female and that in the centre a male (photo: courtesy of Geoff Deacon).

Size matters – especially if you are female

The argument that dingoes could not have caused the extinction of the thylacine is summarized by Johnson: 'thylacines were big. At around 30 kilograms, a thylacine was about twice as heavy as the average dingo, and this should have given it an upper hand' (2006: 158). This argument rests on morphological data from Tasmanian thylacines. Things may have been quite different in Holocene Australia. When brain size is used as a proxy for body size, the data suggest that, while male thylacines were similarly sized to dingoes, female thylacines were considerably smaller. This high degree of dimorphism between male and female thylacines (see Jones 1997) could have rendered female thylacines particularly vulnerable in direct encounters with dingoes, which lack marked sexual dimorphism (Corbett 1995). This vulnerability could then have resulted in lower rates of reproduction, and subsequent decreases in population size. If this decrease in population was also accompanied by encounter competition, in which smaller predators avoid larger species by changing their behaviour to reduce the risk of encounters (Thomson and Gese 2007), thylacine populations could have received a double blow resulting from restricted access to resources (Glen and Dickman 2005).

Invasive predators and naïve prey

While the theory that prey naivety can contribute to the demise of a species has been viewed critically, historical evidence in Australia shows that approximately twenty species of native mammals have gone extinct since 1788 and another ninety-four are considered threatened on a national scale (www.environment.gov.au). These predators' impacts are thought to have been so severe because native Australian species had not co-evolved with them and thus did not possess effective adaptations to detect, avoid and escape these novel predators (Salo et al. 2007). A global meta-analysis of studies investigating the impacts of predators indicate that invasive predators tend to have stronger impacts than native predators, presumably because prey are more vulnerable to a novel predator with which they have not coevolved (Salo et al. 2007).

Invasive predators can also have catastrophic effects on ecosystems by imposing strong selective pressures on species that have evolved in their absence, thereby driving other species to extinction and shaping ecological communities. The meso-predator release hypothesis predicts that larger predators will suppress the abundance of smaller predators through direct killing and competition (Letnic et al. 2011) – effects that are likely to be exacerbated when the larger predator is an invasive species.

Were dingoes and thylacines ecological surrogates?

There has been considerable debate over the ecological niche filled by the thylacine. Many authors have argued that, due to their similar morphology, dingoes and thylacines were ecological surrogates that likely filled a similar ecological role in Australian ecosystems (Corbett 1995; Johnson and Wroe 2003; Wroe et al. 2007). If the two species occupied the same niche this would lend weight to the hypothesis that competition with

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dingoes may have driven thylacines to extinction (Corbett 1995; McNab 2005). However, due to its skull and limb morphology, and the likelihood that it was a solitary forager, others have argued that the thylacine may have preyed upon relatively small prey compared to canids (Jones and Stoddart 1998). Comparison of tooth morphology of dingoes and thylacines from mainland Holocene Australia shows that the strength of the canine, a predictor of prey size (Van Valkenburgh and Ruff 1987), was similar in both thylacines and dingoes (Fig. 2). Male Holocene mainland thylacines, due to their relatively large body size, similarly strong canine teeth and relatively large bite force/body size (Attard et al. in press; Goswami et al. 2001; Wroe et al. 2005, 2007), may have been capable of taking prey of similar size to dingoes. However, owing to their considerably smaller body size, it is likely that female thylacines hunted smaller prey than male thylacines and dingoes. Further, contemporary understanding of the processes of biological invasion and exploitative competition suggest that it is unlikely that resource competition with dingoes could have caused the extinction of the thylacine. This is because there have been no studies documenting competition-driven extinction events (Davis 2003).

Dingoes may also have had a greater impact on native prey species because they were likely to be both smarter and hungrier than thylacines. Placental mammals tend to have higher metabolic rates and larger brains, a correlate of intelligence in many mammals (Deaner et al. 2007), than marsupials of similar body size and life history strategies. For example, metabolic rate in dasyurid marsupials scales with body size in a fashion similar to that of placental carnivores, but is considerably lower than that of similar-sized placental carnivores (McNab 2005). Thus, it is likely that on a per capita basis dingoes may have needed to consume a greater mass of prey than a thylacine of a similar size to meet their daily energy requirements. Dingoes' larger brain size and thus probably higher intelligence may have given dingoes an advantage over thylacines with regard to their relative ability to capture prey. The likely difference in metabolic demand and cognitive abilities between the two predator species and the relative inability of naïve prey species to escape predation by novel predators means that dingoes and thylacines may not have been ecological surrogates. Moreover, in comparison to the thylacine, the dingo's impact on large prey populations may have been exacerbated by that fact that they frequently exist in packs that hunt cooperatively (Thomson 1992).

Contemporary ecological studies indicate that dingoes have dramatic effects on ecosystems communities in Australia, in particular suppressing the abundances of large herbivores and smaller predators (Letnic et al. in press). In turn, grasses and smaller mammals tend to benefit from dingoes' dampening effects on the impacts of herbivores and smaller predators. These effects of dingoes extend to the modern human economy in Australia where sheep grazing and kangaroo harvesting tend not to be conducted in the presence of dingoes due to predation and competition with dingoes, respectively (Letnic et al. in press).

The conclusion that dingoes and thylacines occupied separate ecological niches has significant bearing on the interpretation of the archaeological and fossil records, and warrants particularly close attention given the profound effects that dingoes have on the fauna and flora of contemporary Australian ecosystems (Letnic et al. in press). Using modern ecological studies as a model, it can be expected that the arrival of dingoes,

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which were much more effective and hungry hunters of naïve prey than thylacines, would have precipitated a dramatic decrease in the abundance of large macropods and wombatids, a signal that might be visible in the fossil and archaeological records (Fillios et al. 2010). It might also be expected that the dingo's arrival may have produced a raft of indirect effects on small prey and vegetation owing to their suppressive effects on herbivores and smaller predators consistent with trophic cascade theory (Letnic et al. 2009).

Archaeological evidence

The archaeological record of faunal change in Holocene Australia can be used as an independent test of the hypotheses suggested by the morphological data and modern ecological information for the effects of dingoes. Faunal evidence from a variety of Holocene rock shelters across the continent suggests a shift in the average body size of prey species exploited by Aboriginal people, notably a decrease in the frequency of large mammals and an increase in the frequency of small mammals (Dortch 2004a, 2004b; Dortch and Wright 2010; Morwood 1987). Johnson and Wroe (2003: 944) suggest that this shift could be partly due to a broadening of the resource base to include a larger range of exploited species. We suggest that the introduction of the dingo would also have played a large role in this apparent shift in exploited mammalian species (Fillios et al. 2010), as this pattern is consistent with what might be expected if dingoes were more effective, and hungrier predators than thylacines. In this study the hypothesis that this decrease in prey body size could be a result of human-dingo competition for the same food resources is quantitatively tested by compiling archaeological faunal data from several sites across Australia, and using a hypothesis-testing approach to examine whether there is a correlation between this shift and the arrival of dingoes.

Our statistical analysis of Holocene faunal data indicated a decrease in the frequency of large prey following the arrival of dingo, an effect which increased with increasing rainfall (Fig 1). This finding is consistent with the notion that dingoes were more effective hunters of large prey than thylacines, and that the subsequent reduction in the availability of large prey such as macropods and wombatids following the arrival of the dingo resulted in people increasing their consumption of smaller-bodied prey. In fact, the combination of the morphological and archaeological data suggests that the ecological balance changed with the arrival of dingoes, causing not only the extinction of the thylacine, but potentially a change in human subsistence via prey choice.

The prevailing view is that these changes in species frequencies in the archaeological record are another aspect of Holocene intensification, with some suggesting they may be related to subsistence changes that were in part brought about by the arrival of the dingo (Beaton 1982; Bowdler 1981). Hiscock argued that the new toolkits should be viewed as 'technological solutions to risks created by scheduling uncertainties' (1994: 267). It is possible that the arrival of the dingo influenced human subsistence choice not only through its utility as a hunting tool, but as a competitor for the same resources. This suggestion is not inconsistent with Johnson and Wroe's (2003: 944) proposal that improvements in human hunting technology, coupled with increased population size, might have resulted in decreased population sizes of specific vertebrate species.

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Their hypothesis fits well with these results suggesting that selective predation by dingoes on smaller, female thylacines could also have reduced the reproductive rate of the species. The combined impact of these factors could very plausibly have dealt a fatal blow to a small population.

Conclusion

Implicating the dingo as a driving force behind the extinction of the thylacine from mainland Australia has traditionally rested on a central piece of circumstantial evidence – namely that both the Tasmanian devil and thylacine disappeared from the mainland after the introduction of the dingo, yet persisted on the island of Tasmania where it was never introduced. Based on the new measurements of brain size and canine strength reported in this study, evidence suggests that, while dingoes were similarly sized to male thylacines, they were considerably larger than female thylacines on mainland Australia during the Holocene. Female thylacines would have been particularly susceptible to direct killing by dingoes and such killing could have driven thylacines to extinction if their rate of mortality exceeded the rate of recruitment. Due to their smaller brain, likely lower metabolic rate and convergent morphology, thylacines would have also been susceptible to resource competition with dingoes. These results lend support to the hypothesis that the novel interactions posed by invasive dingoes drove thylacines to extinction on mainland Australia.

This study suggests that the extinction of the thylacine may not have been caused by human intensification or climate change. Rather, the combination of new morphological evidence for Holocene dwarfing of thylacines, coupled with the shift toward smaller-bodied prey in the archaeological faunal record of human occupation sites, suggests that the arrival of dingoes may have led to an ecological regime shift and that dingoes may have played a significant role in the ultimate extinction of the thylacine. While the human element and the intensification of resource use across the continent during the same time period is not discounted, our findings that mainland dingoes were larger than thylacines provides support for a large role played by the dingo, which was until now more speculative than substantive.

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